Distribution of common octopus and common squid paralarvae in a wind-driven upwelling area (Ria of Vigo, northwestern Spain)

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The variation of paralarval abundance in a region subjected to wind-driven upwelling (Ria of Vigo, northwestern Spain) was studied. Research cruises were undertaken during the favourable upwelling season (May to October) in 2000 and 2001. Each cruise included biological and hydrographic sampling and consisted of five stations in waters located to the east and west of the Cies Islands. A total of 221 paralarvae of Octopodidae and Loliginidae were collected over the 12-month study period. During 2000, higher abundance of paralarvae was observed in July, September and October for Loligo vulgaris and Octopus vulgaris. In 2001, abundance of both species was higher in May and also in September for O. vulgaris. The mantle length of the paralarvae varied from 1.25 to 2.25 mm and from 1.00 to 4.90 mm within the O. vulgaris and L. vulgaris individuals, respectively. The presence/absence of upwelling modulates the abundance and spatial distribution of loliginid and octopod paralarvae. The relationship between the distribution and movement of these paralarvae in the Ria of Vigo seems to follow the circulation system defined for this area; when the upwelling extends its influence inside the Ria, the paralarvae are transported to the inner part in a west–east direction.

INTRODUCTION

Cephalopods represent a valuable resource whose commercial importance increases annually (Caddy and Rodhouse, 1998). Integration of environmental and biological data for baseline studies of cephalopod fishery resources remains an incipient field that needs in-depth research. Cephalopod biological oceanographic research has mainly focused on pelagic squid species in relation to oceanic current systems (González *et al.*, 1997; Dawe *et al.*, 2000; Anderson and Rodhouse, 2001; Waluda *et al.*, 2001). Most of these studies have been based on inferring population responses from environmental associations involving recruited squids.

Direct studies of planktonic paralarvae and their response to oceanographic variation are scarce in comparison with other invertebrate larvae and fishes (Boletzky, 2003). The most comprehensive studies of the early life history of cephalopods were carried out in Japanese waters (Okutani and Watanabe, 1983; Bower *et al.*, 1999; Sakurai *et al.*, 2000). In the north-western Atlantic, the highest abundance of planktonic paralarvae was consistently found in the vicinity of the Gulf Stream (Vecchione *et al.*, 2001). The larval phases of pelagic cephalopods in the south-western Atlantic are concentrated on the Patagonian shelf/off-shelf area, and here interannual variability in the physical system may thus have profound effects on the year-class strength of species that are adapted to exploit these features (Rodhouse *et al.*, 1992). The vertical structure of the water column, especially the occurrence of a pycnoclyne and the variable mixed-layer depth were demonstrated to have an important impact on the vertical distribution patterns of cephalopod paralarvae (Röpke *et al.*, 1993). Moreover, *Loligo opalescens* paralarvae increased dramatically in abundance following an El Niño event in central-east Pacific (Zeidberg and Hamner, 2002).

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The western coast of the Iberian Peninsula experiences wind regimes that favour seasonal upwelling from late spring to early autumn. The upwelling originates from either subpolar or subtropical branches of Eastern North Atlantic Central Water (ENACW; Ríos *et al.*, 1992). This water mass enhances the primary production and positive estuarine circulation within the four Ria-type estuaries forming the south-western coastline of Galicia (Prego and Fraga, 1992). This scenario influences the distribution patterns of larvae dynamics (Fusté and Gili, 1991; Riveiro *et al.*, 2004) and reared mussel production (Blanton *et al.*, 1987; *et al.*, Figueiras *et al.*, 2002) and is able to support large sardine fisheries (Guisande *et al.*, 2004). There has been only one short-term study on cephalopod paralarvae in this area, which showed that their abundance and distribution were closely related to the upwelled ENACW (Rocha *et al.*, 1999). A circulation pattern of these paralarvae following upwelling was hypothesized.

The aim of this study is to investigate the distribution of *Octopus vulgaris* and *Loligo vulgaris* paralarvae collected in coastal waters during an extended period. Spatial and temporal differences in abundance were related with different oceanographic conditions.

METHOD

Biological sampling

A total of 17 surveys were undertaken by the R/V *Mytilus* from May to October in 2000 (nine cruises) and 2001 (eight cruises). Biological and hydrographical sampling were undertaken in each survey, which consisted of five stations in waters located east and west of the Cies Islands and in water depths ranging from 35 to 105 m (Fig. 1). Zooplankton samples were collected by towing, from near-bottom to the surface, a 750-mm diameter bongo net of 375-μm mesh. At a ship speed of two knots, the bongo net was lowered and stabilised near the bottom for a period of 10 min and subsequently hauled up at 0.5 ms^{-1}. The bongo net was equipped with a mechanical flow meter to measure the water flow through the net. Paralarvae from two nets were pooled, and all data were standardized to number of paralarvae per 1000 m^{-3}. The zooplankton samples were fixed onboard with 4% buffered formalin for 24 h and preserved in 70% alcohol. Paralarvae were separated and later classified with reference to Sweeney *et al.* (Sweeney *et al.*, 1992) and to a paralarvae reference collection previously obtained from laboratory reared specimens. The mantle length (ML) of 178 *L. vulgaris* and *O. vulgaris* individuals was recorded to the nearest 0.05 mm using a dissecting microscope equipped with a micrometer. A total of 43 paralarvae deformed during collection (e.g. those with damaged or inverted mantles) were not measured.

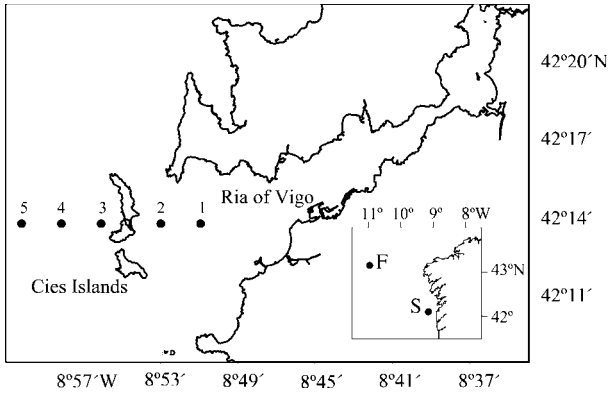

Fig. 1. Map of the study area and the stations surveyed during 2000 and 2001. The fixed stations F (43° N, 11° W) and S (42°07.2′ N, 9°24′ W) are also plotted on the map.

Oceanographic and atmospheric data

Vertical temperature-salinity profiles were obtained in each station using a SEA-BIRD 19 CTD with an accuracy for salinity of ±0.005 and ±0.01°C. No data were obtained in October 2000 because of technical problems. Additional oceanographic data on sea surface temperature (SST) from the Silleiro buoy located at station S, 42°07.2′ N, 9°24′ W (Fig. 1) close to the sampling area were provided by the Spanish agency Puertos del Estado (www.puertos.es). The measurements were taken at a depth of 3 m. Cross-shore (-*Qx*) component of the Ekman transport was calculated by means of geostrophic wind speed obtained from atmospheric pressure fields for position F, 43° N, 11° W (Fig. 1) located 150 miles west of the Galician coast, following the methodology described by Bakun (Bakun, 1973) and adapted for the Iberian Peninsula by Lavín *et al.* (Lavín *et al.*, 1991). Ekman transport is equal to the rate of water upwelled per kilometre of coast and expressed by the upwelling index in m^2s^{-1}. A positive or negative value of -*Qx* indicates favourable (northerly winds) or unfavourable (southerly winds) upwelling conditions, respectively. The presence of prevailing upwelling conditions is assumed when the thermohaline properties of the water can be traced back to those of ENACW.

RESULTS

Figure 2 shows the variability of the mean daily -*Qx* and SST time series for the favourable upwelling months where the cruises were undertaken. Cross-correlation of -*Qx* and SST was significant at a lag of 2–3 days. In 2000, both -*Qx* and SST clearly showed consecutive

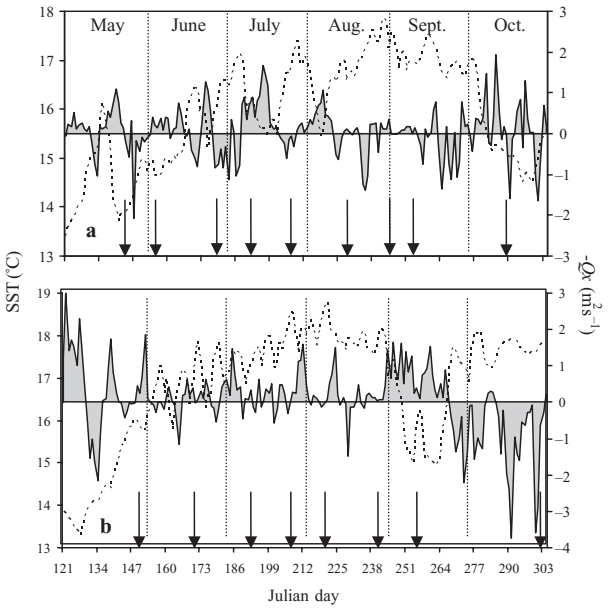

Fig. 2. Time course of the daily cross-shore component of the Ekman transport (shaded area, -*Qx*) and the SST (dotted line) at the fixed station during 2000 (**a**) and 2001 (**b**). Arrows indicate the date of sampling.

upwelling/relaxation pulses from May to mid-August, followed by an extended relaxation period and a further upwelling event in October extending to mid-November. In 2001, two clear events of upwelling occurred in early May and September. During summer, moderate northerly winds provoked a relatively stable relaxation period. From late September southerly winds prevailed causing downwelling. In general, summer 2000 was typified by upwelling. The TS profiles shown in Fig. 3 illustrate representative situations occurring over the period studied, when upwelled waters reached the study area (a), and when this area was not subjected to upwelling conditions. During upwelling, the TS profiles reach the ENACW line which indicates the presence of upwelled waters in the area (Fig. 3a), whilst during relaxation periods or downwelling the TS profiles indicate the absence of upwelled waters in the area. According to the upwelling index in Fig. 2, periods of high upwelling index can be observed (240–265 Julian day, 2001), caused by continuous and intense southward winds which imply favourable upwelling conditions. On the contrary, there were non-upwelling conditions during the calm or low-wind periods (i.e. 280–300 Julian day, 2000) and downwelling events (270–300 Julian day, 2001) provoked by northward winds.

Abundances of *L. vulgaris* in 2000 and 2001 individuals ranged from 0 to 9.03 (1.78 ± 2.376), and from 0 to 6.7 (0.44 ± 1.205) individuals × 1000 m^{-3}, respectively. With respect to *O. vulgaris*, abundances varied from 0 to 5.02

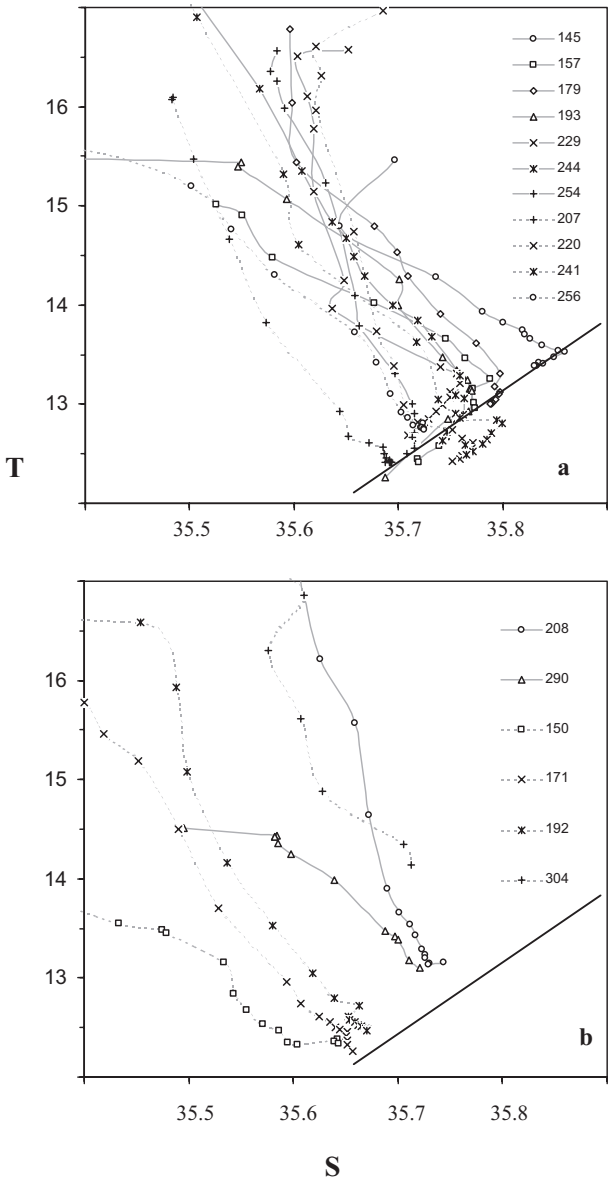

Fig. 3. TS diagrams showing upwelling events (**a**) and non-upwelling (**b**) during the sampling period. Numbers indicate the sampling day (Julian days) shown in Fig. 4. The line corresponds to ENACW water mass.

(1.02 ± 1.438), and from 0 to 7.98 (0.9 ± 1.811) individuals × 1000 m^{-3} in 2000 and 2001, respectively. During 2000, higher abundance of paralarvae was observed in July (Julian days 193 and 208), September (Julian day 254) and October (Julian day 290) for *L. vulgaris* and *O. vulgaris* (Fig. 4a). In 2001, abundance of both species was higher in May (Julian day 150), and also in September (Julian day 256) for *O. vulgaris* (Fig. 4b).

The abundance of *Loligo vulgaris* paralarvae in 2000 was similar in the inner (1 and 2) and outer (3, 4 and 5) stations when the upwelling water penetrated the Ria (Fig. 5a), and

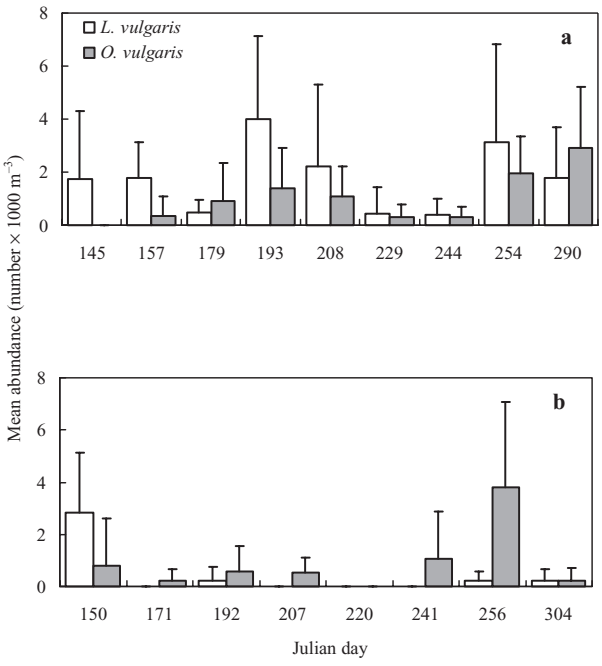

Fig. 4. Mean abundance distribution and standard deviations of cephalopod paralarvae caught in the Cies Islands in each sampling during 2000 (**a**) and 2001 (**b**).

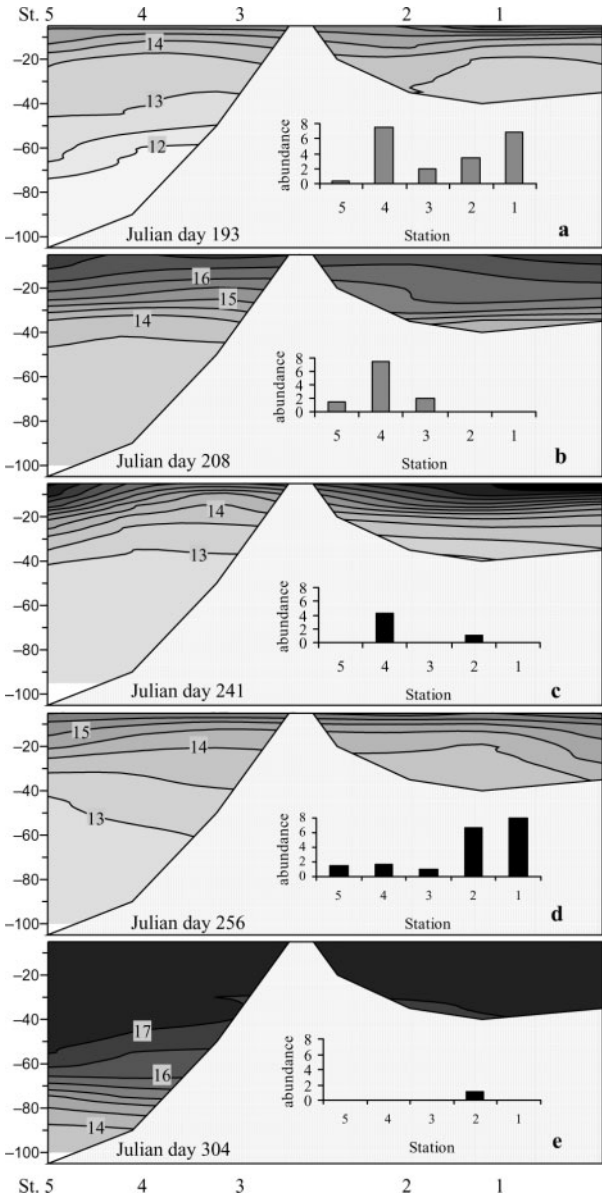

Fig. 5. Water column isotherms in inner and outer stations when upwelling reaches the inner part of the Ria (**a** and **d**), when upwelling is only present in the outer part of the Ría (**b** and **c**) and during downwelling (**e**). Abundance of *Loligo vulgaris* (grey bars) and *Octopus vulgaris* paralarvae (black bars) per station during each sampling date is also presented. Station numbers are denoted at the top and bottom of the figure. Isotherms with a 0.5°C resolution are also included for each sampling date.

was higher in offshore waters when the upwelling did not reach the inner part of the Ria (Fig. 5b). The most remarkable feature is the near absence of common squid paralarvae in 2001 (Fig. 4b). With regard to *Octopus vulgaris*, there are three different situations. When the upwelling is only present in offshore waters, the highest presence of paralarvae was located in the outer stations (Fig. 5c). However, when the upwelling reaches the inner part of the Ría, the paralarvae were present in both the outer and inner stations (Fig. 5d). There was a notable absence of paralarvae during the strong downwelling event that occurred in October 2001 (Figs 2b and 5e).

ML ranged from 1.0 to 4.9 mm (2.32 ± 0.93, n = 58), and from 1.5 to 3.25 mm (2.23 ± 0.51, n = 24) for *L. vulgaris* paralarvae in 2000 and 2001, respectively. Concerning *O. vulgaris*, ML varied from 1.25 to 2.25 mm (1.62 ± 0.199, n = 51) in 2000, and between 1.25 and 2.0 mm (1.6 ± 0.20, n = 45) in 2001.

DISCUSSION

The factors responsible for the recruitment success in cephalopods are most dependent on interactions between the phases of egg mass, hatchling and pre-recruit juveniles and the physical and biological environment prevailing during each phase (Rodhouse *et al.*, 1992). Thus, paralarval surveys must be emphasized as they are fundamental in studying distribution, biology, spawning areas and population structure of cephalopods (Piatkowski, 1998). However, the relatively small samples obtained, and their patchy distributions are the principal limitations in paralarval studies (Piatkowski, 1998; Rocha *et al.*, 1999).

Galician coastal waters are known as an area with an important fishery on loliginid squids (Guerra *et al.*, 1994)

and common octopus (Guerra, 1997). In the north-eastern Atlantic, *L. vulgaris* spawning takes place all year round, with peak abundance of spawners recorded in January and February (Guerra and Rocha, 1994). At a temperature of 10°C, hatching of *L. vulgaris* paralarvae occurs ~70 days after spawning under rearing conditions (Boletzky, 1974). Therefore, it should be expected that the maximum of paralarval abundance in Galicia would be centred from March to July. In 2000, *L. vulgaris* paralarvae appeared mostly in July and September to October (Fig. 4a), the latter originating in a secondary hatching period, summer to autumn (Rocha and Guerra, 1999). In 2001, 84% of the paralarvae of *L. vulgaris* were collected in May and were almost absent for the rest of the year (Fig. 4b). Concerning the north-eastern Atlantic population of *O. vulgaris*, there is a clear peak of spawning in spring but reproductive events range from December through August (Otero *et al.*, 2004). Our results confirm the reproductive pattern in Galician waters, defined by an intense hatching period in autumn arising from the previous spawning in spring (Figs 4a and b). There is only one previous study regarding the abundance of wild *O. vulgaris* paralarvae, that of Sakaguchi *et al.* (Sakaguchi *et al.*, 1999) in Japanese waters. These authors report two peaks of maximum distribution in June and October. However, comparisons between their work and this study should be taken with caution since, although *O. vulgaris* is reported to be a species from tropical, subtropical and temperate waters, its distribution is being redefined to conform modern biogeographical boundaries (Mangold, 1998).

In Galicia, seasonal cycles of upwelling/relaxation and downwelling periods occur as a result of coastal winds with a periodicity of ~10–20 days alternating in all seasons (Álvarez-Salgado *et al.*, 1993; Torres *et al.*, 2003). These situations of stress and relaxation of upwelling determine the depth to which ENCAW rises and its influence on the shelf and inside the Ria. The temperature inside the Ria responds to shelf winds with a delay of ~3 days (Gilcoto *et al.*, 2001). The influence of the upwelling of this water mass on the abundance of paralarvae has been previously observed by Rocha *et al.* (Rocha *et al.*, 1999). Thus, *L. vulgaris* paralarvae increased 44% during the recent upwelling event within few days, while the paralarvae of octopods increased only 10%. These authors hypothesised the relationship between the distribution and movement of cephalopod paralarvae within a circulatory cell in a west–east direction of the upwelling near the coast. In this study, we extend that hypothesis, to include transport of paralarvae to the inner part of the Ria during upwelling following the current system described by Souto *et al.* (Souto *et al.*, 2003). In view of the fact that cephalopod paralarvae show diel-vertical migration (Piatkowski *et al.*, 1993), the current system in the Ria of Vigo during upwelling would help the retention of paralarvae in a circulatory cell, thus allowing them to return near the coast. In upwelling areas, coastal retention appears to be the main environmental factor for *O. vulgaris* recruitment success, whereas upwelling intensity and wind-induced turbulence appear to be secondary beneficial factors (Faure *et al.*, 2000). Other studies in Galicia showed that sardine and decapod larvae are also related to this oceanographic setting (Fusté and Gili, 1991; Santos *et al.*, 2004). The results obtained in this study suggest that this oceanographic regime modulates the abundance of loliginid and octopus paralarvae in a different manner depending on the strength of the upwelled water.

It is clear that the sizes of *Octopus vulgaris* and *Loligo vulgaris* paralarvae are remarkably lower in Galicia than those collected in the wild in other areas and under rearing conditions at higher temperatures (Villanueva, 1995, 2000; Sakaguchi *et al.*, 1999). These size differences are explicable since temperature influences cephalopod growth rate throughout the life cycle. Hatchlings emerging at warmer temperatures have also experienced warmer incubation temperatures during embryonic development, and so hatch at larger sizes (Forsythe, 1993; Pecl *et al.*, 2004).

Owing to the seasonal cycles of the prevailing oceanographic regime in Galician waters and the poorly-understood patchy distribution of cephalopod early life cycles, a fine scale sampling is needed in order to identify the influence of the upwelling intensity and associated retention, as well as the concentration processes, for evaluating the balance between enrichment and its optimal use by the paralarvae of cephalopods.

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